Determinants of differential reproductive allocation in wolf and nursery-web spiders

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Abstract. We used data from 33 species of cursorial spiders in northern Mississippi (USA) to investigate the relative contributions of ecology and phylogeny to the reproductive trade-off between number and size of offspring. Sixty percent of the variation among genera for female reproductive allocation was due to differences between the family Pisauridae and the family Lycosidae. Temporal variation in reproductive allocation during the reproductive season was not observed for the majority of species examined. We found significantly different patterns of reproductive allocation among species within genera, suggesting that each species has responded to distinct selection pressures. Preliminarily, this extensive variation appears to be due mostly to interspecific competition and predation risk from other spiders. However, the patterns of reproductive allocation of species within a single guild (i.e., a group of species potentially competing for the same resources) for the two families are very different. Larger species of wolf spiders (family Lycosidae) within a given guild produce smaller numbers of larger offspring relative to the size of the mother, and smaller species produce the reverse. However, in nursery-web spiders (family Pisauridae) the larger species within a guild produce larger numbers of smaller offspring than expected. The current study provides an example of the flexibility of life history evolution despite phylogenetic constraints. It also demonstrates the potential for varying life history strategies to mediate competition, allowing similar species to coexist.

Keywords: Fecundity, interspecific competition, life-history evolution, Lycosoidea, Pisauridae, predatory dominance, trade-offs

Life history theory predicts a trade-off between the number of offspring produced and the size of those offspring, given the finite amount of resources available to individuals (Stearns 1992; Roff 2002). Females can invest in producing either a larger number of smaller offspring or fewer larger offspring. The observed pattern of maternal resource allocation (few large or many small) may result from environmental influences and/or phylogenetic constraints (Marshall & Gittleman 1994), with natural selection acting to produce a clutch size that maximizes the genetic contribution to the next generation within those constraints (Lack 1947; Stearns 1992; Fox & Czesak 2000). Differences in the way females allocate maternal resources should reflect selective pressures (mortality regimes) specific to the biotic and abiotic environment (Fox & Czesak 2000).

Pisauridae (nursery-web spiders) and Lycosidae (wolf spiders) are closely related families in the superfamily Lycosoidea (Coddington 2005). Species within each family exhibit qualities that make them ideal for testing hypotheses concerning the evolution of the allocation of reproductive resources. First, females exhibit similar but not identical levels of parental care, and offspring of the two families may face differential predation risk due to the mode of maternal care. Maternal care in both families can be divided into pre- and post-emergence stages. During the pre-emergence stage, wolf spider females carry egg sacs suspended from their spinnerets, and nursery-web females carry egg sacs in their chelicerae. The post-emergence stage begins after a period of 4–6 wk for wolf spiders and 2–3 wk for nursery-web spiders (this study), when females must tear open the egg sac in order for spiderlings to

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emerge. In wolf spiders, once the egg sac has been opened the spiderlings emerge and crawl onto their mother's abdomen where they remain for 1–2 wk before dispersing. Nursery-web females, on the other hand, suspend the opened egg sac from a specially constructed 3-dimensional web structure. Emerging spiderlings crawl onto the nursery web and remain there approximately 1–2 wk before dispersing. During this period, the female does not abandon her offspring but remains close by, presumably to defend her young (but see Kreiter & Wise 2001).

Second, the populations we used of these species are semelparous. Inclusion of iteroparous species can introduce confounding effects of trade-offs between current and future reproduction and current reproduction and future survival (e.g., Desouhant et al. 2005; Waelti & Reyer 2007).

Third, species of both families are found in a variety of habitats and are almost exclusively cursorial hunters. Thus, the possibility for extensive adaptation to specific habitats exists as well as the potential for strong competition among species in the same habitats.

In wolf (Araneae: Lycosidae) and nursery-web (Araneae: Pisauridae) spiders in Mississippi, we have shown that a trade-off does exist between size and number of offspring, and that there is no significant variation among species in the proportion of available resources allocated to total reproductive effort (Nicholas et al. 2011). In the current paper, our primary question is: Given the trade-off presented in Nicholas et al. (2011), how do phylogeny, interspecific competition, and temporal heterogeneity in the timing of reproduction interact to determine among-species patterns of maternal resources partitioning between number and size of offspring? Specific hypotheses are: 1) Do species or genera that are more closely evolutionarily related share more similar patterns of reproductive resource allocation? 2) Do potentially competing

species within a guild show consistent patterns of reproductive allocation of resources among guilds? 3) Do individual species shift reproductive resource allocation during the reproductive season?

METHODS

We housed spiders and calculated reproductive output as in Nicholas et al.(2011). Briefly, we used wild-caught females representing 28 morphospecies of wolf spiders from ten genera and five species of nursery-web spiders from two genera. Sample sizes for individual morphospecies can be found in Table 1 of Nicholas et al. (2011).

Measuring fecundity.—We opportunistically collected females with egg sacs throughout Mississippi from March– September 2004–2006. Some gravid females were also captured, but individuals not producing an egg sac within 48 h were not used for the study to avoid the confounding effects of supplemental laboratory feeding. Most of the species included in this study are nocturnal, and we collected at night using a headlamp to locate eye shine. Several of the wolf spider species have not been previously described and we classified them as morphospecies. All together, we collected 28 morphospecies of wolf spiders belonging to the following genera (with number of species in that genus in paretheses): *Allocosa* (1), *Geolycosa* (2), *Gladicosa* (1), *Hogna* (7), *Pardosa* (3), *Pirata* (2), *Rabidosa* (4), *Schizocosa* (6), *Trochosa* (1) and *Varacosa* (1) and five species of nursery-web spiders within the genera *Dolomedes* (3) and *Pisaurina* (2). We deposited voucher specimens in the Mississippi Entomological Museum. The number of individuals per species collected was highly variable, with a mean of 27.7 and a median of five (Nicholas et al. 2011).

We brought females into the laboratory and maintained them individually in plastic containers measuring 22 cm by 15 cm. The containers were filled with several cm of commercial topsoil, and dried grass stems were added to provide places for spiders to perch. We kept larger individuals of Pisauridae in 38-l aquariums filled with several cm of commercial topsoil and 2–3 large sheets of pine tree bark provided as a substrate for nursery web construction. We misted containers every other day to provide moisture. In our experience (Nicholas et al. 2011), females carrying egg sacs did not feed, so that laboratory diet is not a confounding factor on fecundity or resource allocation. Any burrowing behavior, date of egg sac construction, and date of hatching were recorded at each misting or feeding.

We made the following observations for all wolf spiders. When all spiderlings emerged, we weighed the female and her spiderlings to the nearest milligram. The female was then anesthetized with CO_2 gas and the spiderlings were removed using a soft paint brush. We then weighed the female without the spiderlings, and $\geq$ 30 spiderlings were counted and weighed en masse. We collected similar data from nursery-web spiders except that we did not need to anesthetize females or spiderlings because they are living on a nursery web, eliminating the need for anesthetization to remove offspring. For species producing fewer than 100 spiderlings, all offspring were counted directly. We estimated mean spiderling mass, number of offspring (in species with > 100 spiderlings/clutch), and total clutch mass using the following equations:

$$\text{Total clutch mass} = \text{Mass (Female} + \text{spiderlings)}$$
$$- \text{Mass (Female alone)}$$

$$\text{Mean spiderling mass} = \text{Total mass of spiderlings counted/}$$
$$\text{Number of spiderlings counted}$$

$$\text{Total number of offspring} = \text{Total clutch mass/}$$
$$\text{Mean spiderling mass}$$

Ecological community.—We used "ecological community" to identify potentially competing suites of species. Ecological community contains a spatial component (habitat type) and a temporal component (timing of offspring hatching: time of hatching is important because similarly-sized individuals are more likely to compete). We classified habitat type as forest (pine, deciduous, or mixed stands of trees) or grassland. We distinguished three seasons of offspring hatch: spring, summer, or fall. Thus, ecological community describes a guild of spiders that is born in the same season and use the same habitat.

Data analyses.—Contribution of phylogeny. We test the hypothesis that phylogenetic relations influence the patterns of reproductive allocation of resources in the families Lycosidae and Pisauridae. Increasingly, researchers have used comparative methods to examine various patterns of life history traits across species. However, traits measured from related groups may not be independent data points, and phylogenetic relationships should be considered in any comparative study (Freckleton et al. 2002; Blomberg et al. 2003; Desdevises et al. 2003). When not taken into account, phylogenetic autocorrelation can lead to erroneous conclusions concerning the evolution of traits under consideration (Blomberg et al. 2003). As suggested by Stearns (1992), we examined the amount of variance in reproductive allocation at different taxonomic levels using a nested analysis of variance. The taxonomic level explaining the majority of variation in a life history trait provides the most independent level of comparison and reduces the confounding effect of phylogenetic relationships, and thus is the level at which further analyses should be conducted. We conducted a nested analysis of variance with the independent variables of species within genera, genera within family, and family. The independent variable, reproductive allocation, was derived from a principal components analysis of female mass, offspring mass, and number of offspring. This allowed us to identify the components that explicitly describe the trade-off between offspring mass and offspring number (i.e., reproductive allocation) (see Nicholas et al. 2011).

To test whether species within a genus differed significantly in reproductive allocation, we examined separately the three wolf spider genera for which we had data on more than three species (*Hogna*, *Rabidosa*, and *Schizocosa*). Residual offspring mass and number were derived from a least squares linear regression between log female mass and log offspring mass and between female mass and number of offspring. We conducted a separate analysis of variance for each genus, with species as the independent variable and residual offspring mass and residual number of offspring as dependent variables.

Table 1.—Summary of some life history data for species collected. The tabled information includes means and standard errors for: mass of females in mg (Maternal), the mean number of offspring produced per clutch (Fecundity), mean spiderling mass in mg (Offspring mass); as well as classification of ecological community. Species were designated as: 1) hatching in the spring (Sp), summer (Su), or fall (Fl); and 2) found in forest (F) or grassland (G) habitats. Their spatial and temporal separation divided them into ecological communities.

Species	Maternal mass	Fecundity	Offspring mass	Ecological community
Lycosidae				
Allocosa funereal (Hentz 1844)	17	56	0.24	SuG
Geolycosa fatifera (Kurata 1939)	542	118	1.50	SuG
Geolycosa missouriensis (Banks 1895)	742 ± 21	133 ± 18	1.83 ± 0.01	SuG
Gladicosa pulcra (Keyserling 1877)	301 ± 19	164 ± 28	1.13 ± 0.03	SpF
Hogna annexa (Chamberlin & Ivie 1944)	246 ± 13	219 ± 20	0.72 ± 0.02	SuG
Hogna aspersa (Hentz 1844)	1288 ± 125	268 ± 68	2.59 ± 0.08	SuF
Hogna georgicola (Walckenaer 1837)	840 ± 39	236 ± 15	2.19 ± 0.03	SuF
Hogna lenta A	599 ± 37	206 ± 13	2.03 ± 0.07	SuG
Hogna lenta B	642 ± 53	569 ± 61	0.70 ± 0.03	FlG
Hogna wallacei (Chamberlin & Ivie 1944)	544 ± 63	228 ± 45	1.19 ± 0.03	SuG
Hogna watsoni (Gertsch 1934)	140	60	1.01	SuG
Pardosa cocinna (Thorell 1877)	35 ± 2	60 ± 12	0.36 ± 0.01	SuG
Pardosa milvina (Hentz 1844)	20 ± 5	40 ± 3	0.47 ± 0.01	SpG
Pardosa pauxilla (Montgomery 1904)	12	18	0.33	SuF
Pirata species A	12 ± 1	28 ± 3	0.37 ± 0.01	SuG
Pirata species B	35	74	0.24	SuF
Rabidosa carrana (Bryant 1934)	592 ± 145	187 ± 93	1.83 ± 0.19	SpG
Rabidosa hentzi (Banks 1904)	250 ± 33	90 ± 30	1.66 ± 0.17	SuF
Rabidosa punctulata (Hentz 1844)	415 ± 5	143 ± 3	1.36 ± 0.01	SpG
Rabidosa rabida (Walckenaer 1837)	599 ± 12	356 ± 9	1.05 ± 0.01	SuG
Schizocosa avida (Walckenaer 1837)	241 ± 16	212 ± 22	0.50 ± 0.02	SuG
Schizocosa bilineata (Emerton 1885)	66 ± 44	28 ± 5	0.47 ± 0.03	SuG
Schizocosa duplex (Chamberlin 1925)	67 ± 7	76 ± 15	0.57 ± 0.02	SuF
Schizocosa ocreata gr.	70 ± 5	80 ± 7	0.60 ± 0.01	SuF
Schizocosa saltatrix (Hentz 1844)	102 ± 11	116 ± 9	0.65 ± 0.01	SP
Schizocosa uetzi (Stratton 1997)	73	63	0.58	SuF
Trochosa acompa (Montgomery 1902)	88 ± 11	102 ± 13	0.70 ± 0.01	SuG
Varacosa avara (Keyserling 1877)	96 ± 28	73 ± 12	0.95 ± 0.07	SpG
Pisauridae				
Dolomedes albineus (Latreille 1804)	736 ± 129	668 ± 58	0.97 ± 0.02	SuF
Dolomedes tenebrosus (Hentz 1844)	1947	2627	0.59	SuF
Dolomedes triton (Walckenaer 1837)	642 ± 32	1147 ± 530	0.44 ± 0.00	SuG
Pisaurina dubia (Hentz 1847)	50 ± 8	83 ± 15	0.49 ± 0.02	SuF
Pisaurina mira (Walckenaer 1837)	238 ± 12	348 ± 21	0.77 ± 0.03	SuF

Multiple comparisons of mean residual offspring mass and mean residual offspring number were carried out among species within each genus using Tukey-Kramer HSD in order to determine whether and how individual species within a genus differed.

Within species temporal variation. We had samples spanning six or more sampling periods for ten species, and thus we could test for an effect of hatch date on within-species variation in life history traits. Using linear regression adjusting P-values for multiple comparisons (the Bonferroni method), we tested for effects of hatch date on female mass, offspring mass, number of offspring, and total clutch mass.

Testing for the effects of interspecific competition. Four ecological communities contained at least four species from the same family. For those communities, we tested the hypothesis that patterns of reproductive allocation would differ among different-sized species within a guild by performing least-squares linear regression, using female mass as the independent variable and reproductive allocation as the dependent variable.

All statistical analyses were carried out using JMP software version 7.0.

RESULTS

Over 3 yr, we collected and analyzed data from 914 individual spiders of 28 species of wolf spider (10 genera) and five species of nursery-web spider (two genera), summarized in Table 1 and in Nicholas et al. (2011).

Phylogeny and reproductive allocation.—The nested analysis of variance showed that most of the variation in reproductive allocation occurred at the family level, rather than generic level. Reproductive allocation was significantly different between families ($F_{1,10} = 16.6$, $P = 0.0005$) and explained 60% of the variation in reproductive allocation. Genera nested within families was borderline significant ($F_{10,31} = 2.3$, $P = 0.05$) and explained an additional 9% of the variation.

Considering three lycosid genera separately, we found that in each case, species within a genus varied significantly in both residual offspring mass and residual offspring number. Within the genus *Rabidosa,* species category was highly predictive of

Table 2.—Post hoc comparisons of mean residual offspring number (Residuals) within each genus separately. Levels not connected by the same letter are significantly different (Tukey's HSD, $\alpha = 0.05$).

Genus	Species	Levels	Residuals
Hogna	*lenta* B	A	0.375
	annexa	B	0.076
	wallacei	B, C	−0.046
	lenta A	B, C	−0.049
	aspersa	B, C	−0.068
	georgicola	C	−0.069
	watsoni	B, C	−0.361
Rabidosa	*rabida*	A	0.108
	hentzi	A, B	−0.042
	punctulata	B	−0.089
	carrana	A, B	−0.252
Schizocosa	*saltatrix*	A	0.050
	ocreata group	A	0.006
	avida	A, B	−0.003
	duplex	A, B	−0.027
	uetzi	A, B	−0.099
	bilineata	B	−0.328

residual offspring mass ($F_{1,3} = 102.15$, $P < 0.001$) and residual offspring number ($F_{1,3} = 34.57$, $P < 0.0001$). Within the genus *Hogna*, the species category was highly predictive of residual offspring mass ($F_{1,6} = 31.55$, $P < 0.001$) and residual offspring number ($F_{1,6} = 9.31$, $P < 0.001$). Within the genus *Schizocosa*, the species category was highly predictive of residual offspring mass ($F_{1,6} = 10.11$, $P < 0.001$) and less so of residual offspring number ($F_{1,6} = 2.66$, $P = 0.04$). See Table 2 for individual comparisons.

Within-species temporal variation in reproductive allocation.—We examined the relationship between the date of reproduction and female mass, offspring mass, and offspring number among individuals in nine species of wolf spider and one species of nursery-web spider (Table 3). After adjusting for multiple non-independent tests of significance using the Dunn-Šidák method, only one of the 30 regressions was still significant. Further, the mean of the regression slopes was not significantly different from zero for all species combined. The one significant result was for *Hogna lenta sp.* A, where females produced significantly smaller offspring later in the season.

Interspecific competition.—Four ecological communities (see Fig. 1) contained four or more potentially competing species (guilds), that is, species existing in the same habitat type, hatching at a similar time, and observed to feed on the same prey and each other. For each of these four ecological communities (lycosids: SpG, SuF, SuG; pisaurids: SuF), we performed least squares linear regression using reproductive allocation as the independent variable and female mass as the dependent variable to test the hypothesis that reproductive allocation was related to relative body size within a guild (Fig. 1). Among four species of lycosids limited to grassy areas and reproducing in the spring, female mass was positively associated with reproductive allocation, meaning that larger species produced smaller numbers of larger offspring than expected ($r = 0.99$, $df = 2$, $P = 0.01$). For the seven species of lycosids specialized (found only) in forest habitats and reproducing in summer, larger females also produced smaller numbers of larger than expected offspring ($r = 0.83$, $df = 5$, P

Table 3.—Regressions for within season timing of reproduction and the life history traits female mass, mean offspring mass, and offspring number. In each case, time was the independent variable and the life history trait the dependent variable. Sample size (n) was the number of females sampled during the time period. The asterisk denotes the only relationship that was significant after adjusting for multiple tests on non-independent data.

	Species	r^2	n	Sample Period
Female mass	*Pisaurina mira*	0.22	15	22 May–17 June
	Hogna annexa	0.17	20	22 April–11 Sept
	Hogna lenta A	0.39	15	22 May–20 Sept
	Hogna georgicola	0.03	39	8 May–20 Sept
	Pirata A	0.01	8	26 May–27 June
	Schizocosa saltatrix	0.31	7	12 May–16 June
	Pardosa milvina	0.18	14	4 April–8 Aug
	Hogna lenta B	0.47	6	21 Sept–3 Oct
	Varacosa avara	0.21	8	19 April–15 May
	Gladicosa pulchra	0.00	8	3 March–4 April
Offspring mass	*Pisaurina mira*	0.03		
	Hogna annexa	0.01		
	Hogna lenta A	0.51*		
	Hogna georgicola	0.00		
	Pirata A	0.03		
	Schizocosa saltatrix	0.04		
	Pardosa milvina	0.05		
	Hogna lenta B	0.01		
	Varacosa avara	0.00		
	Gladicosa pulchra	0.18		
Offspring number	*Pisaurina mira*	0.46		
	Hogna annexa	0.19		
	Hogna lenta A	0.24		
	Hogna georgicola	0.11		
	Pirata A	0.00		
	Schizocosa saltatrix	0.51		
	Pardosa milvina	0.00		
	Hogna lenta B	0.34		
	Varacosa avara	0.10		
	Gladicosa pulchra	0.04		

$= 0.02$). Among fourteen species of lycosids limited to grassy areas and reproducing in the summer, larger species produced smaller numbers of larger offspring than expected ($r = 0.60$, $df = 12$, $P = 0.02$).

However, for the four species of pisaurids also reproducing during the summer and being found only in forested areas, the relationship between adult body size and mean offspring size was negative ($r = -0.84$, $df = 2$, $P = 0.16$). Although the slope is not statistically different from zero, it is strongly negative rather than positive, as in potentially competing groups of lycosids. Further, the slope for pisaurid species is significantly different from the slope of the three groups of lycosid spiders ($F_{3,23} = 9.60$, $P < 0.05$).

DISCUSSION

We draw three conclusions from our study. First, there is a strong phylogenetic component to the trade-off between offspring size and number among families, within families among genera, and within genera among species. Second, within-season temporal variation in female mass at sexual
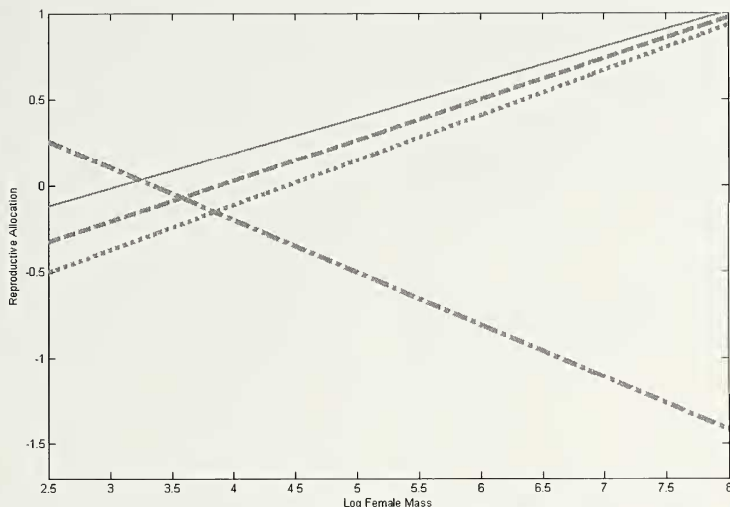
Figure 1.—Linear estimations of the relationship between mean female mass in mg (Log Female Mass) and the principle component axis specifying the trade-off between offspring size and number (Reproductive Allocation). Positive values of the reproductive allocation axis represent species with small numbers of large offspring, and negative numbers represent species with large numbers of small offspring. The three positive slopes represented by the solid, dashed, and dotted lines are all wolf spiders belonging to a particular spider community (SpG, SuF, and SuG respectively), separated in space or time. For wolf spiders, larger species within each guild (SuF) produced relatively few offspring of large size. The negative slope, represented by alternating dashes and dots, represents a guild of nursery web spiders (SuF). Within this community, larger species produced large numbers of relatively small offspring.

maturity, mean offspring mass, and offspring number was observed for only one of the ten species (for offspring mass) for which we had sufficient data. Overall, a clear pattern emerges that female mass, mean offspring mass, and fecundity are constant throughout the breeding season within species. Third, we can draw tentative inferences concerning the effects of competition on reproductive allocation. Female mass was significantly related to patterns of reproductive allocation within potentially competing groups of species (guilds). However, in the Lycosidae larger species within the ecological community produced smaller numbers of larger offspring relative to smaller species. In the Pisauridae, the reverse of this was true, with smaller species producing relatively large numbers of smaller offspring. We elaborate on these conclusions below.

Contribution of phylogeny to patterns of reproductive allocation.—Female reproductive allocation was significantly different between members of the Pisauridae and members of the Lycosidae, showing clear lineage-specific evolution, possibly as the result of different ecological pressures. Family accounted for 60% of the variation in reproductive allocation among genera. The effects of genus nested within family were borderline significant and explained an additional 9% of the variation in reproductive allocation among species. Further, reproductive allocation within the genera *Rabidosa*, *Hogna*, and *Schizocosa* differed significantly among species. The primary result is that members of Pisauridae have significantly larger numbers of smaller offspring than members of

Lycosidae. In general, offspring fitness typically increases with offspring size (review in Fox & Czesak 2000 and see Walker et al. 2003 for a specific example with wolf spiders). However, maximizing the fitness of individual offspring does not necessarily maximize the genetic contribution of the parents to the next generation when there is a trade-off between number and size of offspring (Fox & Czesak 2000).

The smaller offspring of the Pisauridae may be favored in part due to the type of maternal care exhibited in this family. Although the wolf spiders examined carry their egg sac on their spinnerets, build a burrow prior to oviposition (G.E. Stratton unpublished), and remain in the burrow until offspring emerge; the pisaurids carry their egg sac in their chelicerae and do not build burrows. Thus, the pisaurids examined in this study are probably more exposed to potential predators, and while carrying egg sacs are prohibited from using their fangs for defense. Numerous researchers have shown that smaller eggs hatch more quickly (e.g., Fox 1997; Azevedo et al. 1996). In this study, pisaurid eggs hatched on average 18 days post-oviposition while lycosid eggs hatched on average 31 days post-oviposition. This earlier hatch time would lessen the period when pisaurid females and young might be most vulnerable to predation. Thus, selection for smaller eggs and faster development times could be an adaptation to this lineage-specific mode of maternal care.

Simpson (1995) found no effect of maternal care on offspring mass or number of offspring among spiders, including members of the Lycosidae and Pisauridae. However,

he placed lycosids and pisaurids in the same category of maternal care, whereas our results suggest that the specific manner of maternal care is correlated with differences in reproductive allocation, suggesting different selective pressures.

We also found significant differences in reproductive allocation within the three genera with sufficient sample size (*Rabidosa, Hogna,* and *Schizocosa*) to draw inferences. Our data suggest that life history variation among species is due primarily to interspecific competition and predation within ecological communities (see Importance of interspecific competition below).

Within-species temporal variation in reproductive allocation.—We found little support for temporal changes in reproductive allocation within species during the course of the reproductive season. Statistical power for individual regressions was often low (range: 0.28–0.94), but the fact that the pattern was consistent across all ten species and that the mean slopes were not different from zero strongly suggests that allocation to offspring size and number changes little during the season. Only one species, *Hogna lenta A,* showed a significant seasonal reduction in mean offspring mass (see also Reed & Nicholas 2008). Iida & Fujisaki (2007) showed that females of *Pardosa pseudoannulata* (Bösenberg & Strand 1906) produced smaller numbers of larger offspring late in the reproductive season. Larger offspring have been shown to have higher starvation tolerance and are able to develop more quickly into advanced instars, both of which are traits that have been shown to increase overwintering survival in spiders (Martyniuk & Wise 1985; Iida 2005). *Hogna lenta A,* however, showed the opposite pattern in that larger numbers of smaller offspring were produced late in the reproductive season. It is unclear whether such a reduction is adaptive or perhaps related to a non-significant trend toward smaller females reproducing later in the season.

Importance of interspecific competition.—Our data suggest that interspecific competition, including intraguild predation, might play important roles in the evolution of life history and phenology of species within ecological communities of these spiders. 1) Among three ecological communities of wolf spiders, we found a repeatable pattern of increasing resource provisioning to individual offspring at the expense of numbers of offspring for larger species within guilds. The pattern appears to be the opposite for nursery-web spiders, with larger females producing larger than expected numbers of smaller offspring. However, we have sampled only one such community of nursery-web spiders. 2) Species within the genera *Rabidosa, Hogna,* and *Schizocosa* show considerable variation in reproductive allocation and phenology, suggesting niche partitioning within ecological communities and the evolution of divergent phenologies among species within genera to reduce niche overlap. We elaborate on these two points below.

The similar patterns of reproductive allocation among the three communities of wolf spiders (Fig. 1) suggest two alternative explanations: resource partitioning within species among age classes and among species for each age class, or life-history consequences of intraguild predation. The ability for resource partitioning to produce this pattern depends on to what extent spiders switch to larger prey as they grow larger, as compared to just adding larger prey to their prey base at

smaller sizes. Zimmerman & Spence (1989) found the former in *Dolomedes triton* (Walckenaer 1837), and Okuyama (2007) found the latter in two species of jumping spider. The same pattern of changes in reproductive allocation with changes in adult size could potentially arise under strong intra-guild predation if the smallest species produce offspring so small that they are below the threshold that triggers predation in larger species, if smaller species produce sufficient numbers of offspring to satiate intra-guild predators, or if sufficiently smaller offspring are too fast for larger species to capture (Rypstra & Samu 2005).

Prior research has indicated that juvenile wolf spiders suffer very high intraguild predation. For five species of wolf spiders, other species of spider made up 7.7 ± 0.9% of the diet, with cannibalism accounting for a similar percentage (Hallander 1970; Yeargan 1975; Reed et al. 2007a,b; Reed & Nicholas 2008). Although we have data on only two species, many species within *Rabidosa, Hogna,* and *Schizocosa* occupy similar habitats, and all are generalist carnivores, a diet that includes conspecifics as well as congeners (Reed et al. unpublished data). Thus, the potential exists for both competition for resources and competition through intraguild predation to be powerful selective forces. Unfortunately, there are no clear differential predictions for the outcome of resource competition versus intraguild predation.

It is interesting to note that *Hogna lenta* B had an extremely unusual reproductive allocation pattern for a wolf spider. This species is the only grasslands species reproducing in the fall (Table 1), and it produced unusually large numbers of offspring of small size, similar to a pisaurid species. This provides anecdotal support for the hypothesis that competition and/or the potential for intraguild predation is a major force in the evolution of offspring size, and that the optimum size is quite different under conditions of less intense competition from other cursorial spiders.

The four species of nursery-web spider that form a guild show a very different relationship between female mass and reproductive allocation. In this guild, large species produce unexpectedly large numbers of small offspring. The only detailed study of diet in a nursery-web spider is a study on *Dolomedes triton* (Zimmerman 1989). Other spiders made up 2.9 ± 0.1% of *D. triton's* diet, with almost no cannibalism. The level of intra-guild predation in this one data set is significantly less than for any of the five wolf spider species examined, providing preliminary evidence that guilds of nursery-web spiders generally suffer lower levels of intraguild predation and cannibalism than wolf spiders and, that this could be a contributing factor in the differences in reproductive allocation between the families.

Models of interspecific competition predict competitive exclusion when two or more species reach a certain level of overlap in resource utilization (Hardin 1960; MacArthur & Levins 1967). Hutchinson (1961), however, suggested that competitors with a high degree of overlap in resource utilization could in fact coexist if the competitive advantage shifted seasonally between the competitors. Support for Hutchinson's hypothesis has been shown in several spiders. Balfour et al. (2003) found seasonal shifts in competitive advantage (i.e., predatory dominance) between the wolf spiders *Pardosa milvina* (Hentz 1844) and *Hogna helluo*

(Gertsch 1934). Spiller (1984) found a similar shift between two species of orb-weaving spider, *Metepeira grinnelli* (Coolidge 1910) and *Cyclosa turbinate* (Walckenaer 1842). Our results suggest that competitive and predatory interactions may select for asynchronous phenologies as well as influence the pattern of reproductive allocation among the species examined.

Rabidosa rabida, *R. hentzi*, and *R. punctulata* are all found in open grasslands, and all three exploit resources in a similar manner, climbing to the top of grass stems to wait for arthropod prey. There is a high degree of diet overlap between *R. punctulata* and *R. rabida* (niche overlap on the diet axis between these two species is 0.93; Reed et al. unpublished). The heavy overlap in resource utilization among these species creates the potential for intense interspecific competition. Detailed field observations over a three-year period suggest that asynchronous phenology and differences in reproductive allocation may provide an important mechanism allowing coexistence among these members of *Rabidosa* (Reed and Nicholas 2008). However, whether the differences in phenology and reproductive allocation observed in *Rabidosa* evolved due to competition or are a prior adaptation that allows coexistence among these species is unknown. Future work involving manipulation of species composition in experimental plots is needed (Connell 1980).

We have shown that reproductive allocation with respect to offspring size and number is significantly different between the closely related families Lycosidae and Pisauridae. Further, we show that despite strong phylogenetic conservatism among genera within a family, species within genera are varied in their allocation of reproductive resources and apparently respond to differential selection pressures for the offspring size and number continuum. In particular, intraguild competition and predation may be important factors impacting cursorial spider life history evolution and community structure. However, conclusions concerning the importance of completion are tentative and will require further research.

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